

**BIOGRAPHICAL SKETCH**

Provide the following information for the key personnel in the order listed for Form Page 2.  
Follow the sample format for each person. **DO NOT EXCEED FOUR PAGES.**

NAME Raymond M. Welsh, Ph.D.		POSITION TITLE Professor of Pathology, Molecular Genetics & Microbiology	
EDUCATION/TRAINING <i>(Begin with baccalaureate or other initial professional education, such as nursing, and include postdoctoral training.)</i>			
INSTITUTION AND LOCATION	DEGREE <i>(if applicable)</i>	YEAR(s)	FIELD OF STUDY
University of Massachusetts, Amherst	B.S.	1967	Microbiology
University of Massachusetts, Amherst	Ph.D.	1972	Micro/Virology
University of Kansas, Lawrence	Post-Doc	1972-1973	Micro/Biochemistry
Scripps Clinic & Research Foundation, La Jolla, CA	Post-Doc	1973-1975	Virology/Immunology

**A. Positions and Honors.****Positions and Employment**

- 1972-1973 Visiting Assistant Professor of Microbiology, Univ. of Kansas, Lawrence, KS; Dept. of Microbiology
- 1975-1980 Assistant Member, Scripps Clinic and Research Foundation, La Jolla, CA; Dept. of Immunopathology
- 1979 Visiting Scientist, Karolinska Institute; Scripps Clinic, 1987.
- 1980 Adjunct Associate Professor of Pathology, Univ. California at San Diego Medical School, Dept. of Pathology,
- 1980-1985 Associate Professor of Pathology, Molecular Genetics and Microbiology, Univ. Mass. Medical School, Worcester, MA
- 1985-Present Professor of Pathology, Molecular Genetics and Microbiology, Univ. Mass. Medical School, Worcester, MA

**Honors, Editorial Boards, and Advisory Groups:**

Recipient of RCDA AI-00253 (1978-1983); Editorial Boards: J. Immunol. (1982-1986; 1997-present) Section Editor (2001); Proc. Soc. Exp. Biol. Med. (1978-1987); J. Virol. (1986-1989; 1991-present; Editor for Immunology and Pathogenesis 1998-present); Natural Immunity Cell Growth Regulation (1984-2000); J. Natl. Cancer Inst. (1987-1991); J. Exp. Med. (1995-present); Virology (1996-present); Study Sections: American Cancer Society (National) Immunology and Immunotherapy Section (1988-1991); American Cancer Society (Massachusetts) (1981-1991), Chairman (1985-1991); State of California AIDS Task Force (1985-1996); NIH Virology (1991-1995).

**B. Selected peer-reviewed publications (of 193 publications).**

- Selin, L.K., K. Vergilis, R.M. Welsh and S.R. Nahill. 1996. Reduction of otherwise remarkably stable virus-specific cytotoxic T lymphocyte (CTL) memory by heterologous viral infections. J. Exp. Med. 183:2489-2499.
- Zarozinski, C.C. and R.M. Welsh. 1997. Minimal bystander activation of CD8 T cells during the virus-induced polyclonal T cell response. J. Exp. Med. 185:1629-1639.
- Tay, C.-H. and R.M. Welsh. 1997. Distinct organ-dependent mechanisms for the control of murine cytomegalovirus infection by natural killer cells. J. Virol. 71:267-275.
- Ciupito, A.T., M. Petersson, C.L. O'Donnell, K. Williams, S. Jindal, R. Kiessling and R.M. Welsh. 1998. Immunization with an LCMV peptide mixed with heat shock protein 70 results in protective anti-viral immunity and specific CTLs. J. Exp. Med. 187:685-691.

- Szomolanyi-Tsuda, E., Q.P. Le, R.L. Garcea, and R.M. Welsh. 1998. T cell-independent IgG responses in vivo are elicited by live virus infection, but not by immunization with viral proteins or virus-like particles. *J. Virol.* 72:6665-6670.
- Varga, S.M., and R.M. Welsh. 1998. Cutting Edge: Detection of a high frequency of virus-specific CD4<sup>+</sup> T cells during acute infection with LCMV. *J. Immunol.* 161:3215-3218.
- Lin, M.Y., and R.M. Welsh. 1998. Analysis of the stability of T cell receptor (TCR) repertoire usage during lymphocytic choriomeningitis virus (LCMV) infection of mice. *J. Exp. Med.* 188:1993-2005.
- Lohman, B.L., and R.M. Welsh. 1998. Apoptotic regulation of T cells and absence of immune deficiency in virus-infected IFN- $\gamma$  receptor knock-out mice. *J. Virol.* 72:7815-7821.
- Selin, L.K., S.M. Varga, I.C. Wong, and R.M. Welsh. 1998. Protective heterologous antiviral immunity and enhanced immunopathogenesis mediated by crossreactive memory T cell populations. *J. Exp. Med.* 188:1705-1715.
- Selin, L.K., M.Y. Lin, K.A. Kraemer, D.M. Pardoll, J.P. Schneck, S.M. Varga, P. Santolucito, A.K. Pinto, and R.M. Welsh. 1999. Attrition of T cell memory: selective loss of LCMV epitope-specific memory CD8 T cells following infections with heterologous viruses. *Immunity* 11:733-742.
- Welsh, R.M., T.G. Marquees, B.A. Woda, K.A. Daniels, M.A. Brehm, J.P. Mordes, D.L. Greiner, A.A. Rossini. 2000. Virus-induced abrogation of transplantation tolerance induced by donor-specific transfusion and anti-CD154 antibody. *J. Virol.* 74:2210-2218.
- Zarozinski, C.C., J.M. McNally, B.L. Lohman, K.A. Daniels, and R.M. Welsh. 2000. Bystander sensitization to activation-induced cell death as a mechanism of virus-induced immunosuppression. *J. Virol.* 74:3650-3658.
- Selin, L.K., P.A. Santolucito, A.K. Pinto, and R.M. Welsh. 2001. Innate immunity to viruses: control of vaccinia virus infection by  $\gamma\delta$  T cells. *J. Immunol.* 166:6784-6794.
- Daniels, K.A., G. Devora, W.C. Lai, C.L. O'Donnell, M. Bennett, and R.M. Welsh. 2001. Murine cytomegalovirus is regulated by a discrete subset of natural killer cells reactive with monoclonal antibody to Ly49H. *J. Exp. Med.* 194:29-44.
- McNally, J.M., C.C. Zarozinski, M.Y. Lin, Brehm, M.A., Chen, H.D. and R.M. Welsh. 2001. Attrition of bystander T cells during virus-induced T cell and interferon responses. *J. Virol.* 75:5965-5976.
- Varga, S.M., Selin, L.K., and R.M. Welsh. 2001. Independent regulation of T cell memory pools: relative stability of CD4 memory under conditions of CD8 memory T cell loss. *J. Immunol.* 166:1554-1561.
- Welsh, R.M. 2001. Assessing CD8 T cell number and dysfunction in the presence of antigen. *J. Exp. Med.* 193:19-22.
- Chen, H.D., A.E. Fraire, I. Joris, M.A. Brehm, R.M. Welsh, and L.K. Selin. 2001. Memory CD8<sup>+</sup> T cells in heterologous antiviral immunity and immunopathology in the lung. *Nat. Immunol.* 2:1067-1076.
- Welsh, R.M. and L.K. Selin, 2002. No one is naive: The significance of heterologous T cell immunity. *Nature Rev. Immunol.* 2:417-426.
- Brehm, M.A., A.K. Pinto, K.A. Daniels, J.P. Schneck, R.M. Welsh, L.K. Selin, 2002. T cell immunodominance and maintenance of memory regulated by unexpectedly cross-reactive pathogens. *Nature Immunol.* 3:627-634.
- Kim, S.-K., M.A. Brehm, R.M. Welsh, and L.K. Selin. 2002. Dynamics of memory T cell proliferation under conditions of heterologous immunity and bystander stimulation. *J. Immunol.* 169: 90-98.
- Brehm, M.A., T.G. Marquees, K.A. Daniels, D.L. Greiner, A.A. Rossini, and R.M. Welsh. 2003. Direct visualization of cross-reactive effector and memory allo-specific CD8 T cells generated in response to viral infections. *J. Immunol.* 170:4077-4086.
- Wang, X.Z., S.E. Stepp, M.A. Brehm., H.D. Chen, L.K. Selin, and R.M. Welsh. 2003. Virus-specific CD8 T cells in peripheral tissues are more resistant to apoptosis than those in lymphoid organs. *Immunity* 18:631-642.
- Zipris, D., R.M. Welsh, J.P. Mordes, J.X. Xie, D.L. Greiner, and A.A. Rossini. 2003. Infections that induce autoimmune diabetes in BBDR rats modulate CD4<sup>+</sup> CD25<sup>+</sup> T regulatory cell populations. *J. Immunol.* 170:3592-3602.

Peacock, C.D., S -K. Kim, and R. M. Welsh. 2003. Memory T cell attrition: reduced capacity of bona-fide memory CD44<sup>hi</sup> CD8<sup>+</sup> T cells to respond to homeostatic and poly I:C-induced proliferation. J. Immunol. 171:0000-0000 (in press).

## CURRICULUM VITAE

Raymond M. Welsh, Jr.  
S.S. No. 029-32-4074

### Personal Data:

Date of birth: December 28, 1945  
Place of birth: Montague City, Massachusetts

### Education:

University of Massachusetts, Amherst, B.S., 1967 (Microbiology)  
University of Miami, Coral Gables, 1967-1968 (Microbiology)  
Rensselaer Polytechnic Institute, Troy, N.Y., June 1971  
December 1971 (Biology/Virology)  
University of Massachusetts, Amherst, Ph.D., 1972 (Microbiology/Virology)

### Professional Record:

Biologist, U.S. Army Natick Laboratories, Natick, MA, Feb. 1968-Sept. 1968.  
Postdoctoral Research Assoc., Dept. of Microbiology, Univ. of Kansas, Lawrence, Kansas, Feb. 1972-Aug. 1973.  
Visiting Assistant Professor, Univ. of Kansas, Aug. 1972-May 1973.  
Research Fellow, Dept. of Exp. Pathol., Scripps Clinic and Research Foundation, La Jolla, CA, July 1973-Dec. 1973.  
Assistant Member I Dept. of Immunopathol., S.C.R.F., July 1975-June 1977.  
Assistant Member II Dept. of Immunopathol., S.C.R.F., July 1977-June 1980.  
Visiting Scientist, Dept. of Tumor Biology, Karolinska Institute, Stockholm, Sweden, Oct. 1979-Dec. 1979.  
Adjunct Associate Professor, Dept. of Pathology, Univ. of California at San Diego, La Jolla, CA, March 1980-Sept. 1980.  
Associate Professor, Dept. of Pathology and the Dept. of Molecular Genetics and Microbiology, University of Massachusetts Medical School, Worcester, MA 01605, July

1980-June 1985.

Professor, Dept. of Pathology and the Dept. of Molecular Genetics and Microbiology,  
University of Massachusetts Medical School, Worcester, MA, 10605, July 1985-present.

Chairman, Interdepartmental Immunology and Virology program at UMMC (1992-  
1994; 1983-84); Vice-Chairman (1990-1992);

Visiting Scientist, Scripps Clinic, La Jolla, CA, 3/87-8/87.

Research Awards:

NIH AI-17672, Immunity and Virus Disease, 1974-2004,  
Principal Investigator

NIH NS-12428, Pathogenesis of MS and ALS, 1973-1980,  
Co Investigator.

NIH AI-00253, Maintenance of Chronic Virus Disease,  
1978-1983, Research Career Development Award.

NIH CA-34461, Regulation of Natural Killer Cells,  
1983-2005, Principal Investigator

NIH AM-35506, Virus-Induced Immunopathology, 1985-2004,  
Principal Investigator

NIH AI07349, Training in Immunology, 1992-2007,  
Principal Investigator (Training Grant).

Professional Organizations:

American Association of Immunologists  
American Society of Microbiology  
Society for Experimental Biology and Medicine

Boards and Committees:

Editorial Board, Journal of Immunology, (1980-1984) (1997-Present) Proceedings of the  
Society for Experimental Biology and Medicine, (1977-1988), Natural Immunity and Cell  
Growth Regulation (1983-present), Journal of Virology (1986-1988; 1991-present,  
Editor, 1997-present), J Natl Cancer Inst (1988-1990), Virology (1996-Present)

Arenavirus study group of the International Committee on Virus Nomenclature.

Grant Review study section of the Massachusetts Chapter of the American Cancer Society, 1981-1991; Chairman 1985-1991. Chairman of ACS Professional Scientific Advisory Committee (1994-1998)

Grant Review study section of the State of California AIDS Task Force, 1985-1996.

Grant Review National ACS study section: Immunology and Immunotherapy, 1988-1991.

NIH Virology Study Section, 1991-1995.

### TEACHING EXPERIENCE

1968-69 Teaching assistant for general microbiology laboratory and for virology laboratory courses (Department of Microbiology, UMass, Amherst).

1972-73 Twice taught complete 40 lecture course in general microbiology to undergraduates (Department Microbiology, U. Kansas). Seminar course on slow virus infections (KU).

1980 Participated in laboratory course in virology for medical students at U.Cal., San Diego.

1981-present Courses at the University of Massachusetts Medical Center:

Medical student microbiology - an average of 9 lectures/year in immunology, virology, and bacteriology.

Graduate student virology - coordinator and major lecturer each year - 20 hr. lectures per year.

Graduate student advanced immunology - 3 hours of lectures/year.

## BIBLIOGRAPHY

R.M. Welsh

### Papers:

1. Welsh, R.M., R.S. Trowbridge, J.B. Kowalski, C.M. O'Connell and C.F. Pfau. 1971. Amantadine hydrochloride inhibition of early and late stages of lymphocytic choriomeningitis virus-cell interactions. *Virology*, 45:679-686.
2. Welsh, R.M. and C.J. Pfau. 1972. Determinants of lymphocytic choriomeningitis interference. *J. Gen. Virol.*, 14:177-187.
3. Welsh, R.M. 1972. Defective-interfering lymphocytic choriomeningitis virus. Doctoral dissertation, Univ. of Mass., Amherst.
4. Staneck, L.D., R.S. Trowbridge, R.M. Welsh, E.A. Wright and C.J. Pfau. 1972. Arenaviruses: cellular response to long-term in vitro infection with Parana and lymphocytic choriomeningitis viruses. *Infect. Immun.*, 6:444-450.
5. Pfau, C.J., R.S. Trowbridge, R.M. Welsh, L.D. Staneck and C.M. O'Connell. 1972. Arenaviruses: inhibition by amantadine hydrochloride. *J. Gen. Virol.*, 14:209-211.
6. Welsh, R.M., C.M. O'Connell and C.J. Pfau. 1972. Properties of defective lymphocytic choriomeningitis virus. *J. Gen. Virol.*, 17:355-359.
7. Pfau, C.J., R.M. Welsh and R.S. Trowbridge. 1973. Plaque assays and current concepts of regulation in arenavirus infections. In: F. Lehmann-Grube, ed., *Lymphocytic Choriomeningitis Virus and Other Arenaviruses*, Springer Verlag, New York, pp. 101-111.
8. Oldstone, M.B.A., R.M. Welsh and B.S. Joseph. 1975. Pathogenic mechanisms of tissue injury in persistent viral infections. *Ann. N.Y. Acad. Sci.*, 256:65-72.
9. Welsh, R.M., N.R. Cooper, F.C. Jensen and M.B.A. Oldstone. 1975. Human serum lyses RNA tumor viruses. *Nature*, 257:612-614.
10. Welsh, R.M., P.A. Burner, J.J. Holland, M.B.A. Oldstone, H.A. Thompson and L.P. Villarreal. 1976. A comparison of biochemical and biological properties of standard and defective lymphocytic choriomeningitis virus. *Int. Symp. on Arenaviral Infections of Public Health Importance*, Atlanta, GA, W.H.O. Bull., 52:403-408.

11. Jensen, F.C., R.M. Welsh, N.R. Cooper and M.B.A. Oldstone. 1976. Lysis of oncornaviruses by human serum. 8th Int. Cong. of Assoc. for Comparative Res. on Leukemia, Copenhagen, Oct. 1975. *Bibl. Haematol.*, 43:438-440.
12. Oldstone, M.B.A., L.H. Perrin and R.M. Welsh. 1976. Potential pathogenic mechanisms of injury in amyotrophic lateral sclerosis. In: J.M. Andrews, R.T. Johnson, M.A.B. Brazier, eds., *Amyotrophic Lateral Sclerosis: Recent Research Trends*, No. 19, Academic Press, New York, pp. 251-262.
13. Welsh, R.M., P.W. Lampert, P.A. Burner and M.B.A. Oldstone. 1976. Antibody-complement interactions with purified lymphocytic choriomeningitis virus. *Virology*, 73:59-71.
14. Welsh, R.M., F.C. Jensen, N.R. Cooper and M.B.A. Oldstone. 1976. Inactivation and lysis of oncornaviruses by human serum. *Virology*, 74:432-440.
15. Holland, J.J., L.P. Villarreal, R.M. Welsh, M.B.A. Oldstone, D. Kohne, R. Lazzarini and E. Scolnick. 1976. Long term persistent vesicular stomatitis virus and rabies virus infection of cells *in vitro*. *J. Gen. Virol.*, 33:193-211.
16. Zinkernagel, R.M. and R.M. Welsh. 1976. H-2 compatibility requirement for virus-specific T-cell mediated effector functions *in vivo*. I. Specificity of T cells conferring antiviral protection against lymphocytic choriomeningitis virus is associated with H-2K and H-2D. *J. Immunol.*, 117:1495-1520.
17. Cooper, N.R., F.C. Jensen, R.M. Welsh, Jr. and M.B.A. Oldstone. 1976. Lysis of RNA tumor viruses by human serum: Direct antibody independent triggering of the classical complement pathway. *J. Exp. Med.*, 144:970-984.
18. Welsh, R.M. Jr. 1977. Host cell modification of lymphocytic choriomeningitis virus and Newcastle disease virus altering viral inactivation by human complement. *J. Immunol.*, 118:348-354.
19. Oldstone, M.B.A., J. Holmstoen and R.M. Welsh, Jr. 1977. Alterations of acetylcholine enzymes in neuroblastoma cells persistently infected with lymphocytic choriomeningitis virus. *J. Cell. Physiol.*, 91:459-472.
20. Welsh, R.M., P.W. Lampert and M.B.A. Oldstone. 1977. Prevention of virus-induced cerebellar disease by defective-interfering lymphocytic choriomeningitis virus. *J. Infect. Dis.*, 136:391-399.
21. Merigan, T.C., M.B.A. Oldstone and R.M. Welsh. 1977. Interferon production during lymphocytic choriomeningitis virus infection of nude and normal mice. *Nature*, 268:67-68.



22. Welsh, R.M. and M.B.A. Oldstone. 1977. Inhibition of immunologic injury of cultured cells infected with lymphocytic choriomeningitis virus: Role of defective interfering virus in regulating viral antigenic expression. *J. Exp. Med.*, 145:1449-1468.
23. Welsh, R.M., Jr. and R.M. Zinkernagel. 1977. Heterospecific cytotoxic cell activity induced during the first three days of acute lymphocytic choriomeningitis virus infection in mice. *Nature*, 268:646-648.
24. Welsh, R.M., Jr. 1978. Cytotoxic cells induced during lymphocytic choriomeningitis virus infection of mice: 1. Characterization of natural killer cell induction. *J. Exp. Med.*, 148:163-181.
25. Burton, P.R., J. Steuckemann, R.M. Welsh and D. Paretsky. 1978. Some ultrastructural effects of persistent infections by the rickettsia *C. burneti* in mouse L cells and green monkey kidney (Vero) cells. *Infect. Immun.*, 21:556-566.
26. Welsh, R.M. 1978. Mouse natural killer cells: induction, specificity and function. *J. Immunol.*, 121:475-481.
27. Welsh, R.M., R.M. Zinkernagel and L.A. Hallenbeck. 1979. Cytotoxic cells induced during lymphocytic choriomeningitis virus infection of mice. II. Specificities of the natural killer cells. *J. Immunol.*, 122:475-481.
28. Welsh, R.M. and M.J. Buchmeier. 1979. Protein analysis of defective interfering lymphocytic choriomeningitis virus and persistently infected cells. *Virology*, 96:503-515.
29. Cooper, N.R. and R.M. Welsh. 1979. Antibody and complement dependent viral neutralization. *Springer Semin. Immunopathol.*, 2:285-310.
30. Welsh, R.M. and R.W. Kiessling, 1980. Natural killer cell response to lymphocytic choriomeningitis virus in beige mice. *Scand. J. Immunol.*, 11:363-367.
31. Kiessling, R. and R.M. Welsh. 1980. Killing of normal cells by activated mouse natural killer cells: evidence for two patterns of genetic regulation of lysis. *Int. J. Cancer*, 25:611-615.
32. Welsh, R.M. and L.A. Hallenbeck. 1980. Effect of virus infections on target cell susceptibility to natural killer cell-mediated lysis. *J. Immunol.*, 124:2491-2497.
33. Kiessling, R., E. Erickson, L.A. Hallenbeck and R.M. Welsh. 1980. A comparative analysis of the cell surface properties of activated versus endogenous mouse natural killer cells. *J. Immunol.*, 125:1551-1557.

34. Welsh, R.M. and R.W. Kiessling. 1980. Activated natural killer cells induced during the lymphocytic choriomeningitis virus infection in mice. *In*: R. Herberman, editor, *Natural Cell-Mediated Immunity Against Tumors*, Academic Press, NY, pp. 671-685.
35. Welsh, R.M. and R.W. Kiessling. 1980. Modification of target sensitivity to activated mouse NK cells by interferon and virus infections. *In*: R. Herberman, editor, *Natural Cell-Mediated Immunity Against Tumors*, Academic Press, New York, pp. 963-972.
36. Hansson, M., R. Kiessling and R.M. Welsh. 1980. Interaction between NK cells and normal tissue: definition of an NK-sensitive thymocyte population. *In*: R. Herberman, ed., *Natural Cell-Mediated Immunity Against Tumors*, Academic Press, New York, pp. 855-872.
37. Buchmeier, M.J., R.M. Welsh, F.J. Dutko and M.B.A. Oldstone. 1980. The virology and immunobiology of lymphocytic choriomeningitis virus infection. *Adv. Immunol.*, 30:275-331.
38. Zinkernagel, R.M., A. Althage, E. Waterfield, B. Kindred, R. Welsh, G. Callahan and P. Pincetl. 1980. Restriction specificities, alloreactivity and allotolerance expressed by T cells from nude mice reconstituted with H-2 compatible thymus grafts. *J. Exp. Med.*, 151:376-399.
39. Zinkernagel, R.M., R.M. Welsh, G. Callahan and A. Althage. 1980. On the immunocompetence of H-2 incompatible irradiation bone marrow chimeras. *J. Immunol.*, 124:2356-2365.
40. Altman, A., J.M. Cardenas, R.M. Welsh, Jr. and D.H. Katz. 1980. The biological effects of allogeneic effect factor on T lymphocytes. III. Interferon does not contribute to the biological activities displayed by AEF on both T and B lymphocytes. *Ann. Inst. Pasteur Immunol.*, 131C:335-347.
41. Welsh, R.M. and M.V. Haspel. 1977. Meeting Report. Membrane viruses and immune responses. *Clin. Immunol. Immunopathol.* 8:150-155.
42. Hansson, M., R. Kiessling, B. Andersson and R.M. Welsh. 1980. Effect of interferon and interferon inducers on the NK sensitivity of normal mouse thymocytes. *J. Immunol.*, 125:2225-2231.
43. Welsh, R.M. and W.F. Doe. 1980. Cytotoxic cells induced during lymphocytic choriomeningitis virus infection of mice. III. Natural killer cell activity in cultured spleen leukocytes concomitant with T cell dependent immune interferon production. *Infect. Immun.*, 30:473-483.

44. Welsh, R.M. 1981. Natural killer cells in virus infections. *Curr. Top. Microbiol. Immunol.*, 92:83-106.
45. Welsh, R.M., Karre, M. Hansson, L.A. Kunkel and R.W. Kiessling. 1981. Interferon-mediated protection of normal and tumor target cells against lysis by mouse natural killer cells. *J. Immunol.*, 126:219-225.
46. Kunkel, L.A. and R.M. Welsh. 1981. Metabolic inhibitors render "resistant" target cells sensitive to natural killer cell mediated lysis. *Int. J. Cancer*, 27:73-79.
47. Welsh, R.M. 1981. Do natural killer cells play a role in virus infections? *Antiviral Res.*, 1:5-12.
48. Yogeewaran, G., A. Gronberg, M. Hansson, T. Dalianis, R. Kiessling and R.M. Welsh. 1981. Correlation of glycosphingolipids and sialic acid in YAC-1 lymphoma variants with their sensitivity to natural killer cell mediated lysis. *Int. J. Cancer*, 28:517-526.
49. Biron, C.A. and R.M. Welsh. 1982. Activation and role of natural killer cells in virus infections. *Med. Microbiol. Immunol.*, 170:155-172.
50. Yogeewaran, G., R. Fujinami, R. Kiessling and R.M. Welsh. 1982. Interferon induced alterations in cellular sialic acid and glycoconjugates. Correlation with susceptibility to activated natural killer cells. *Virology*, 121:363-371.
51. Yogeewaran, G., R.M. Welsh, A. Gronberg, R. Kiessling, M. Patarrayo, G. Klein, M. Gidlund, H. Wigzell and K. Nilsson. 1982. Surface sialic acid of tumor cells inversely correlated with susceptibility to natural killer cell mediated lysis. *In*: R.B. Herberman, ed., *NK Cells and Other Natural Effector Cells*, Vol. 2. Academic Press, New York, pp. 765-770.
52. Biron, C.A. and R.M. Welsh. 1982. Proliferation and role of natural killer cells during viral infection. *In*: R.B. Herberman, ed., *NK Cells and Other Natural Effector Cells*, Academic Press, New York, pp. 493-498.
53. Welsh, R.M., C.A. Biron, J.F. Bukowski, S. Habu, M.V. Haspel, K. Holmes, K. Okumura and D.C. Parker. 1983. Regulation and role of natural cell-mediated immunity during virus infections. *In*: F.A. Ennis, ed., *Human Immunity to Viruses*, Academic Press, New York, pp. 21-41.
54. Welsh, R.M. 1984. Natural killer cells and interferon. *CRC Crit. Rev. Immunol.*, 5:55-93.

55. Yogeewaran, G., A. Gronberg, R.M. Welsh and R.W. Kiessling. 1983. Interferon-induced increase in neuraminidase releasable sialic acid and glycosphingolipid metabolism in mouse lymphoma and L1210 leukemic cell lines: correlation with susceptibility to natural killer cell mediated lysis. *Int. J. Cancer*, 31:501-508.
56. Biron, C.A. and R.M. Welsh. 1982. Blastogenesis of natural killer cells during viral infection in vivo. *J. Immunol.*, 129:2788-2795.
57. Bukowski, J.F., C.A. Biron and R.M. Welsh. 1983. Elevated natural killer cell-mediated cytotoxicity, plasma interferon and tumor cell rejection in mice persistently infected with lymphocytic choriomeningitis virus. *J. Immunol.*, 131:991-996.
58. Biron, C.A., G. Sonnenfeld and R.M. Welsh. 1984. Interferon induces natural killer cell blastogenesis in vivo. *J. Leukocyte Biol.*, 35:31-37.
59. Biron, C.A., L.R. Turgiss and R.M. Welsh. 1983. Increase in NK cell number and turnover rate during acute virus infection. *J. Immunol.*, 131:1539-1545.
60. Bukowski, J.F., B.A. Woda, S. Habu, K. Okumura and R.M. Welsh. 1983. Natural killer cell depletion enhances virus synthesis and virus induced hepatitis in vivo. *J. Immunol.*, 131:1531-1538.
61. Welsh, R.M., C.A. Biron and J.F. Bukowski. 1984. The interplay between NK cells and virus infections. D. Schlessinger, ed., *Microbiology-1984*, American Society of Microbiology, Washington, D.C. pp. 320-323.
62. McIntyre, K.W., J.F. Bukowski and R.M. Welsh. 1985. Exquisite specificity of adoptive immunization in arenavirus-infected mice. *Antiviral Res.*, 5:299-305.
63. Woda, B.A., M.L. McFadden, R.M. Welsh and K.M. Bain. 1984. Separation and isolation of rat natural killer (NK) cells from T cells with monoclonal antibodies. *J. Immunol.*, 132:2183-2184.
64. Biron, C.A., S. Habu, K. Okumura and R.M. Welsh. 1984. Lysis of uninfected and virus infected cells in vivo: a rejection mechanism in addition to that mediated by natural killer cells. *J. Virol.*, 50:698-707.
65. Bukowski, J.F., B.A. Woda and R.M. Welsh. 1984. Pathogenesis of murine cytomegalovirus infection in natural killer cell depleted mice. *J. Virol.*, 52:119-128.
66. Bukowski, J.F. and R.M. Welsh. 1985. Interferon enhances the susceptibility of virus-infected fibroblasts to cytotoxic T cells. *J. Exp. Med.*, 161:257-262.
67. Bukowski, J.F., J.R. Warner, G. Dennert and R.M. Welsh. 1985. Adoptive transfer studies demonstrating the antiviral effect of natural killer cells in vivo. *J. Exp. Med.*,

68. Yang, H., G. Yogeewaran, J.F. Bukowski and R.M. Welsh. 1985. Expression of asialo GM<sub>1</sub> and other antigens and glycolipids on natural killer cells and spleen leukocytes in virus-infected mice. *Nat. Immun. Cell Growth Regul.*, 4:21-39.
69. Welsh, R.M., J.F. Bukowski and C.A. Biron. 1985. Regulation of virus infections by natural killer cells. *Fed. Proc.* (In Press).
70. Welsh, R.M., C.A. Biron, J.F. Bukowski, K.W. McIntyre and H. Yang. 1984. Role of natural killer cells in virus infections of mice. *Surv. Synth. Pathol. Res.*, 3:409-431.
71. Bukowski, J.F. and R.M. Welsh. 1985. Inability of interferon to protect virus-infected cells against lysis by natural killer (NK) cells correlates with NK cell-mediated antiviral effects *in vivo*. *J. Immunol.*, 135:3537-3541.
72. Yang, H., I. Joris, G. Majno and R.M. Welsh. 1985. Necrosis of adipose tissue induced by sequential infections with unrelated viruses. *Am. J. Pathol.*, 120:173-177.
73. Holmes, K.V., R.M. Welsh and M.V. Haspel. 1986. Natural cytotoxicity against mouse hepatitis virus-infected target cells. I. Correlation of cytotoxicity with virus binding to leukocytes. *J. Immunol.*, 136:1446-1453.
74. Welsh, R.M., M.V. Haspel, D.C. Parker and K.V. Holmes. 1986. Natural cytotoxicity against mouse hepatitis virus infected cells. II. A cytotoxic cell with a B lymphocyte phenotype. *J. Immunol.*, 136:1454-1460.
75. Yang, H. and R.M. Welsh. 1986. Induction of alloreactive cytotoxic T lymphocytes by acute virus infection of mice. *J. Immunol.*, 136:1186-1193.
76. Biron, C.A., R.J. Natuk and R.M. Welsh. 1986. Generation of large granular T lymphocytes *in vivo* during viral infection. *J. Immunol.*, 136:2280-2286.
77. Welsh, R.M., C.A. Biron, J.F. Bukowski, K.W. McIntyre, R.J. Natuk and H. Yang. 1986. Regulation of viral infections by large granular lymphocytes. *In: Leukocytes and Host Defense*, Alan R. Liss, Inc., NY pp. 403-410.
78. Biron, C.A., K.F. Pedersen and R.M. Welsh. 1986. Purification and target cell range of *in vivo*-elicited blast natural killer cells. *J. Immunol.*, 137:463-471.

79. Biron, C.A. and R.M. Welsh. 1986. Antigenic distinctions and morphological similarities between proliferating NK and cytotoxic T cells. In: E. Lotzova and R.B. Herberman, eds., *Natural Immunity, Cancer and Biological Response Modification*. S. Karger AG, Basel pp. 289-297.
80. Bukowski, J.F. and R.M. Welsh. 1986. The role of natural killer cells and interferon in resistance to acute infection of mice with herpes simplex virus type 1. *J. Immunol.*, 136:3481-3485.
81. Welsh, R.M. 1986. Regulation of virus infections by natural killer cells. *Nat. Immun. Cell Growth Regul.*, 5:169-199.
82. Welsh, R.M. 1986. Regulation of virus infections by cytotoxic leukocytes. *Clin. Immunol. Newsletter*, 7:171-175.
83. Yang, H. and R.M. Welsh. 1986. Induction of allospecific and virus-specific memory cytotoxic T cells during arenavirus infections. *Med. Microbiol. Immunol.*, 175:137-139.
84. Welsh, R.M. 1987. Regulation and role of large granular lymphocytes in arenavirus infections. *Curr. Top. Microbiol. Immunol.*, 134:185-209.
85. Bukowski, J.F. and R.M. Welsh. 1986. Enhanced susceptibility to cytotoxic T lymphocytes of target cells isolated from virus-infected or interferon-treated mice. *J. Virol.*, 59:735-739.
86. Bukowski, J.F. and R.M. Welsh. 1986. Virus-induced interferon modulates susceptibility of tissue to attack by T cells and NK cells. In, *Interferons as Cell Growth Inhibitors and Antitumor Factors*, Alan R. Liss, Inc., N.Y. pp. 175-184.
87. Natuk, R.J., K.W. McIntyre and R.M. Welsh. 1987. Infiltration and chemotaxis of natural killer/large granular lymphocytes during virus infection. *Prog. Leukocyte Biol.*, 6:41-50.
88. Natuk, R.J. and R.M. Welsh. 1987. Accumulation and chemotaxis of natural killer/large granular lymphocytes to sites of virus replication. *J. Immunol.*, 138:877-883.
89. McIntyre, K.W. and R.M. Welsh. 1986. Accumulation of natural killer and cytotoxic T large granular lymphocytes in the liver during virus infection. *J. Exp. Med.*, 164:1667-1681.
90. Biron, C.A., K.F. Pedersen and R.M. Welsh. 1987. Aberrant T cells in beige mutant mice. *J. Immunol.*, 138:2050-2056.

91. McIntyre, K.W., R.J. Natuk, C.A. Biron, K. Kase, J. Greenberger and R.M. Welsh. 1988. Blastogenesis and proliferation of large granular lymphocytes in non-lymphoid organs. *J. Leukocyte Biol.*, 43:492-501.
92. Natuk, R.J. and R.M. Welsh. 1987. Chemotactic effect of human recombinant interleukin-2 on mouse activated large granular lymphocytes. *J. Immunol.*, 139:2737-2743.
93. Bukowski, J.F., K.W. McIntyre, H. Yang and R.M. Welsh. 1987. Natural killer cells are not required for interferon-mediated prophylaxis against vaccinia or murine cytomegalovirus infections. *J. Gen. Virol.*, 68:2219-2222.
94. Welsh, R.M., H. Yang and J.F. Bukowski. 1988. The role of interferon in the regulation of virus infections by cytotoxic lymphocytes. *Bioessays*, 8:10-13.
95. Welsh, R.M., R.J. Natuk, K.W. McIntyre, H. Yang, C.A. Biron and J.F. Bukowski. 1988. Factors influencing the control of virus infections by natural killer cells. In: C. Reynolds and R. Wiltout, eds., *Functions of the Natural Immune System*, Plenum Publishing Corp., N.Y. pp. 111-128.
96. Welsh, R.M., H. Yang and K.W. McIntyre. 1988. Function of natural killer cells in lymphocytic choriomeningitis infection. In: C. Lopez, ed., *Immunobiology and Pathogenesis of Persistent Virus Infections*. American Society of Microbiology, Washington, D.C. pp. 125-134.
97. Yang, H. and R.M. Welsh. 1988. Induction of allospecific cytotoxic T cells by virus infections in vivo. In: P. Ivanyi, ed., *MHC + X. Complex Formation and Antibody Induction*, Springer-Verlag, Berlin, pp. 1-6.
98. Bukowski, J.F., H. Yang and R.M. Welsh. 1988. The antiviral effect of lymphokine-activated killer (LAK) cells. 1. Characterization of the effector cells mediating prophylaxis. *J. Virol.*, 62:3642-3648.
99. Natuk, R.J., J.F. Bukowski and R.M. Welsh. 1989. Antiviral effect of lymphokine-activated killer (LAK) cells. 2. Chemotaxis and homing to sites of infection. *J. Virol.*, 63:4969-4971.
100. Yang, H., P.L. Dundon, S.R. Nahill and R.M. Welsh. 1989. Virus-induced polyclonal cytotoxic T lymphocyte stimulation. *J. Immunol.*, 142:1710-1718.
101. Welsh, R.M., P.L. Dundon, E.E. Eynon, J.O. Brubaker, G.C. Koo and C.L. O'Donnell. 1990. Demonstration of the antiviral role of natural killer cells in vivo with a natural killer cell-specific monoclonal antibody (NK 1.1). *Nat. Immun. Cell Growth Regul.*, 9:112-120.

102. Welsh, R.M., W.K. Nishioka, R. Antia and P.L. Dundon. 1990. Mechanism of killing by virus-induced cytotoxic T cells elicited in vivo. *J. Virol.*, 64:3726-3733.
103. Welsh, R.M. 1990. Methods for studying mouse natural killer cells. In: M.B.A. Oldstone, ed., *Viral Pathogenesis: A Practical Approach*. IRL Press Ltd., Oxford, England, pp. 121-135.
104. Welsh, R.M. and H.R. Robinson. 1993. Infection of immune cells by viruses. In: I.V. Roitt and P.J. Delves, eds., *Encyclopedia of Immunology*, Academic Press Ltd., London, Vol 3, 1560-1562.
105. Brubaker, J.O., K.T. Chong and R.M. Welsh. 1991. Lymphokine-activated killer (LAK) cells are rejected in vivo by activated natural killer cells. *J. Immunol.*, 147:1439-1444.
106. Welsh, R.M., J.O. Brubaker, M. Vargas-Cortes, and C.L. O'Donnell. 1991. Natural killer (NK) cell response to virus infections in mice with severe combined immunodeficiency. The stimulation of NK cells and the NK cell-dependent control of virus infections occur independently of T and B cell function. *J. Exp. Med.*, 173:1053-1063.
107. Welsh, R.M. and M. Vargas-Cortes. 1992. Regulation and role of natural killer cells in virus infections. In: C.E. Lewis and J.O'D.M. Gee, eds., *The Natural Immune System. The Natural Killer Cell*. IRL Press, Oxford, pp 107-150.
108. Welsh, R.M. and H.I. McFarland. 1993. Mechanisms of viral pathogenesis. In: N.S. Young, ed., *Viruses and Bone Marrow*, Marcel Dekker, New York, pp. 3-30.
109. Nishioka, W.K. and R.M. Welsh. 1992. Inhibition of cytotoxic T lymphocyte-induced target cell DNA fragmentation, but not lysis, by inhibitors of DNA topoisomerases I and II. *J. Exp. Med.* 175:23-27.
110. Guberski, D.L., V.A. Thomas, W.R. Shek, A.A. Like, E.S. Handler, A.A. Rossini, J.E. Wallace and R.M. Welsh. 1991. Induction of Type I diabetes by Kilham's rat virus in diabetes-resistant BB/Wor rats. *Science* 254:1010-1013.
111. Vargas-Cortes, M., C.L. O'Donnell, M.C. Appel, K.S. Yurkunis and R.M. Welsh. 1992. A lymphocyte differentiation and activation antigen, CZ-1, that distinguishes between CD8<sup>+</sup> and unstimulated CD4<sup>+</sup> T lymphocytes. *Eur. J. Immunol.* 22:1043-1047.
112. Welsh, R.M. 1993. Lymphocytic choriomeningitis virus-general features. In: R.G. Webster and A. Granoff, eds., *Encyclopedia of Virology*. W.B. Saunders Co., Orlando, FL, pp. 801-811.



113. Vargas-Cortes, M., C.L. O'Donnell, J.W. Maciaszek and R.M. Welsh. 1992. Generation of "NK-escape" variants of Pichinde virus during acute and persistent infections. *J. Virol.* 66:2532-2535.
114. Welsh, R.M., P.R. Rogers and R.R. Brutkiewicz. 1993. Class I MHC antigens and the control of virus infections by NK cells. In, M.V. Sitkovsky and P. Henkart, Eds., *Cytotoxic Cells: recognition, effector functions, generation, and methods*, Birkhauser (Springer/Verlag), Boston, pp. 400-406.
115. McFarland, H.L., S.R. Nahill, J.W. Maciaszek and R.M. Welsh. 1992. CD11b (Mac-1): A marker for CD8<sup>+</sup> cytotoxic T cell activation and memory in virus infection. *J. Immunol.* 149:1326-1333.
116. Brutkiewicz, R.R., S.J. Klaus and R.M. Welsh. 1992. Window of vulnerability of vaccinia virus-infected cells to natural killer cell-mediated cytotoxicity correlates with enhanced NK cell triggering and is concomitant with a decrease in H-2 Class I antigen expression. *Natural Immun.* 11:203-214.
117. Nahill, S.R., and R.M. Welsh. 1992. Polyclonality of the cytotoxic T lymphocyte response to virus infection. *Proc. Soc. Exp. Biol. Med.* 200:453-457.
118. Nishioka, W.K., and R.M. Welsh. 1993. B cells induce apoptosis via a novel mechanism in fibroblasts infected with mouse hepatitis virus. *Natural Immun.* 12:113-127.
119. Brutkiewicz, R.R., C.L. O'Donnell, J.W. Maciaszek, R.M. Welsh, and M. Vargas-Cortes. 1993. The mAb CZ-1 identifies a mouse CD45-associated epitope expressed on IL-2-responsive cells. *Eur. J. Immunol.* 23:2427-2433.
120. Nahill, S.R., and R.M. Welsh. 1993. High frequency of cross-reactive cytotoxic T lymphocytes elicited during the virus-induced polyclonal CTL response. *J. Exp. Med.* 177:317-327.
121. Razvi, E.S., and R.M. Welsh. 1993. Programmed cell death of T lymphocytes during acute viral infection: a mechanism for virus-induced immune deficiency. *J. Virol.* 67:5754-5765.
122. Brown, D.W., R.M. Welsh, and A.A. Like. 1993. Infection of peripancreatic lymph nodes but not islets precedes Kilham rat virus-induced diabetes in BB/Wor rats. *J. Virol.* 67:5873-5878.
123. Kurilla, M.G., S. Swaminathan, R.M. Welsh, E. Kieff, and R.R. Brutkiewicz. 1993. Effects of virally expressed interleukin-10 on vaccinia virus infection in mice. *J. Virol.* 67:7623-7628.

124. Selin, L.K., S.R. Nahill, and R.M. Welsh. 1994. Cytotoxic T cell cross-reactivity between heterologous viruses during acute viral infections. *J. Exp. Med.* 179:1933-1943.
125. Szomolanyi-Tsuda, E., P.L. Dundon, I. Joris, L.D. Shultz, B.A. Woda, and R.M. Welsh. 1994. Acute, lethal NK cell-resistant myeloproliferative disease induced by polyomavirus in SCID mice. *Am. J. Pathol.* 144:359-371.
126. Nishioka, W.K., and R.M. Welsh. 1994. Susceptibility to CTL-induced apoptosis is a function of the proliferative status of the target. *J. Exp. Med.* 179:769-774.
127. Welsh, R.M., C.L. O'Donnell, and L.D. Shultz. 1994. Antiviral activity of NK1.1<sup>+</sup> natural killer cells in C57BL/6 SCID mice infected with murine cytomegalovirus. *Natural Immun.* 13:239-245.
128. Moore, T.A., M. Vargas-Cortes, R.M. Welsh, M. Bennett, and V. Kumar. 1994. Expression of CZ-1: a CD45RB epitope on progenitors of natural killer and other hematopoietic cells. *Scand. J. Immunol.* 39:257-266.
129. Selin, L.K., and R.M. Welsh. 1994. Specificity and editing by apoptosis of virus-induced CTL. *Curr. Opin Immunol.* 6:553-559.
130. Tay, C.-H., R.M. Welsh, and R. R. Brutkiewicz. 1995. Natural killer cell response to viral infections in  $\beta_2$ -microglobulin deficient mice. *J. Immunol.* 154:780-789.
131. Welsh, R.M., L.K. Selin, and E.S. Razvi. 1995. Role of apoptosis in the regulation of virus-induced T cell responses, immune suppression, and memory. *J. Cell. Biochem.* 59:135-142.
132. Brutkiewicz, R.R., and R.M. Welsh. 1995. Major histocompatibility complex Class I antigens and the control of viral infections by natural killer cells. *J. Virol.* 69:3967-3971.
133. Razvi, E., R.M. Welsh, and H.I. McFarland. 1995. The in vivo state of antiviral cytotoxic T lymphocyte precursors: characterization of a cycling cell population containing CTLp in immune mice. *J. Immunol.* 154:620-632.
134. Zarozinski, C.C., E.F. Fynan, L.K. Selin, H.L. Robinson and R.M. Welsh. 1995. Protective CTL-dependent immunity and enhanced immunopathology in mice immunized by particle bombardment with DNA encoding an internal virion protein. *J. Immunol.* 154:4010-4017.
135. Razvi, E.S., Z. Jiang, B.A. Woda and R.M. Welsh. 1995. Lymphocyte apoptosis during the silencing of the immune response to acute viral infections in normal, *lpr*, and Bcl-2-transgenic mice. *Am. J. Pathol.* 147:79-91.
136. Varga, S.M. and R.M. Welsh. 1996. The CD45RB-associated epitope defined by

- monoclonal antibody CZ-1 is an activation and memory marker for mouse CD4 T cells. *Cell. Immunol.* 167:56-62.
137. Selin, L.K., K. Vergilis, R.M. Welsh and S.R. Nahill. 1996. Reduction of otherwise remarkably stable virus-specific cytotoxic T lymphocyte (CTL) memory by heterologous viral infections. *J. Exp. Med.* 183:2489-2500.
  138. Szomolanyi-Tsuda, E. and R.M. Welsh. 1996. T cell-independent antibody-mediated clearance of polyoma virus in T cell-deficient mice. *J. Exp. Med.* 183:403-411.
  139. Welsh, R.M. and G.C. Sen. 1996. Non-specific host responses to viral infections. In: N. Nathanson, ed., *Viral Pathogenesis*. Lippincott-Raven Publishers, NY., pp. 109-142.
  140. Welsh, R.M., C.-H. Tay, S.M. Varga, C.L. O'Donnell, K.L. Vergilis, and L.K. Selin. 1996. Lymphocyte-dependent 'natural' immunity to virus infections mediated by both natural killer and memory T cells. *Seminars in Virology*. 7:95-102.
  141. Zarozinski, C.C., and R.M. Welsh. 1997. Minimal bystander activation of CD8 T cells during the virus-induced polyclonal T cell response. *J. Exp. Med.* 185:1629-1639.
  142. Lohman, B.L., E.S. Razvi and R.M. Welsh. 1996. T lymphocyte down regulation following acute viral infection is not dependent on CD95 (Fas) receptor/ligand interactions. *J. Virol.* 70:8199-8203.
  143. Tay, C.-H., and R.M. Welsh. 1997. Distinct organ-dependent mechanisms for the control of murine cytomegalovirus infection by natural killer cells. *J. Virol.* 71:267-275.
  144. Selin, L.K., and R.M. Welsh. 1997. Cytolytically active memory CTL present in lymphocytic choriomeningitis virus (LCMV)-immune mice after clearance of virus infection. *J. Immunol.* 158:5366-5373.
  145. Welsh, R.M., and R.T. Woodland. 1998. "Viruses, infection of immune cells by." In: *Encyclopedia of Immunology*, Academic Press Ltd. pp 2484-2487.
  146. Karre, K., and R.M. Welsh. 1997. Viral decoy vetoes killer cell. *Nature* 386:446-447.
  147. Ciupitu, A.-M.T., M. Petersson, C.L. O'Donnell, K. Williams, S. Jindal, R. Kiessling, and R.M. Welsh. 1998. Immunization with a lymphocytic choriomeningitis virus peptide mixed with heat shock protein 70 results in protective antiviral immunity and specific cytotoxic T lymphocytes. *J. Exp. Med.* 187:685-691.
  148. Welsh, R.M., M.-Y. Lin, B.L. Lohman, S.M. Varga, C.C. Zarozinski, and L.K. Selin. 1997.  $\alpha\beta$  and  $\gamma\delta$  T-cell networks and their roles in natural resistance to viral

infections. *Immunol. Rev.* 159:79-93.

149. Tay, C.-H., E. Szomolanyi-Tsuda and R.M. Welsh. 1998. Control of infections by NK cells. *Curr. Topics Microbiol. Immunol.* 230:193-220.
150. Selin, L.K., S.M. Varga, I.C. Wong, and R.M. Welsh. 1998. Protective heterologous antiviral immunity and enhanced immunopathogenesis mediated by crossreactive memory T cell populations. *J. Exp. Med.* 188:1105-1715
151. Varga, S.M., and R.M. Welsh. 1998. Stability of virus-specific CD4+ T cell frequencies from acute infection into long term memory. *J. Immunol.* 161:367-374.
152. Welsh, R.M., C.L. O'Donnell, D.J. Reed, and R.P. Rother. 1998. Evaluation of the GAL $\alpha$ 1-3 GAL epitope as a host modification factor eliciting natural humoral immunity to enveloped viruses. *J. Virol.* 72:4650-4656.
153. Lohman, B.L., and R.M. Welsh. 1998. Apoptotic regulation of T cells and absence of immune deficiency in virus-infected IFN- $\gamma$  receptor knock-out mice. *J. Virol.* 72:7815-7821.
154. Lin, M.Y., and R.M. Welsh. 1998. Stability and Diversity of T cell receptor (TCR) repertoire usage during lymphocytic choriomeningitis virus (LCMV) infection of mice. *J. Exp. Med.* 188:1993-2005
155. Szomolanyi-Tsuda, E., and R.M. Welsh. 1998. T cell-independent anti-viral antibody responses. *Curr. Opin. Immunol.* 10:431-435.
156. Szomolanyi-Tsuda, E., Q.P. Le, R. L. Garcea, and R.M. Welsh. 1998. T cell-independent IgG responses in vivo are elicited by live virus infection, but not by immunization with viral proteins or virus-like particles. *J. Virol.* 72:6665-6670.
157. Varga, S.M., and R.M. Welsh. 1998. Cutting Edge: Detection of a high frequency of virus-specific CD4+ T cells during acute infection with LCMV. *J Immunol.* 161:3215-3218.
158. Welsh, R.M. Lymphocytic choriomeningitis virus as a model for the study of cellular immunology. 1999. In, M. W. Cunningham and R. J. Fujinami, eds, *Effects of microbes on the immune system*. Lippincott, Williams and Wilkins, Philadelphia, pp. 280-312.
159. Selin, L.K., M.Y. Lin, S.M. Varga, and R.M. Welsh. 1999. CD8 memory to viruses and the T cell network. In: M.V. Sitkovsky and P.A. Henkart, Eds, *Cytotoxic cells: Basic mechanisms and medical applications*. Lippincott, Williams and Wilkins, Philadelphia, pp. 327-362.
160. Tay, C.-H., L.Y.Y. Yu, V. Kumar, L. Mason, J.R. Ortaldo, and R.M. Welsh. 1999. The role of LY49 NK cell subsets in the regulation of murine cytomegalovirus infections. *J.*

Immunol. 162:718-726.

161. Welsh, R.M., and J.M. McNally. 1999. Immune deficiency, immune silencing, and clonal exhaustion of T cell responses during viral infections. *Curr. Opin. Microbiol.* 2:382.
162. Selin, L.K., M.Y. Lin, K.A. Kraemer, D.M. Pardoll, J.P. Schneck, S.M. Varga, P. Santolucito, A.K. Pinto, and R.M. Welsh. 1999. Attrition of T cell memory: selective loss of LCMV epitope-specific memory CD8 T cells following infections with heterologous viruses. *Immunity* 11:733-742.
163. Welsh, R.M., T.G. Markees, B.A. Woda, K.A. Daniels, M.A. Brehm, J.P. Mordes, D.L. Greiner, A.A. Rossini. 2000. Virus-induced abrogation of transplantation tolerance induced by donor-specific transfusion and anti-CD154 antibody. *J. Virol.* 74:2210-2218.
164. Peacock, C.D., M.Y. Lin, J.R. Ortaldo, and R.M. Welsh. 2000. The virus-specific and allospecific CTL response to lymphocytic choriomeningitis virus is modified in a subpopulation of CD8<sup>+</sup> T cells co-expressing the inhibitory major histocompatibility complex class I receptor Ly49G2. *J. Virol.* 74:7032-7038.
165. Zarozinski, C.C., J.M. McNally, B.L. Lohman, K.A. Daniels, and R.M. Welsh. 2000. Bystander sensitization to activation-induced cell death as a mechanism of virus-induced immune suppression. *J. Virol.* 74:3650-3658.
166. Szomolanyi-Tsuda, E., J.D. Brien, J.E. Dorgan, R.M. Welsh, and R.L. Garcea. 2000. The role of CD40-CD154 interaction in antiviral T cell-independent IgG responses. *J. Immunol.* 164:5877-5882.
167. Selin, L.K., P.A. Santolucito, A.K. Pinto, and R.M. Welsh. 2001. Innate immunity to viruses: control of vaccinia virus infection by  $\gamma\delta$  T cells. *J. Immunol.* 166:6784-6794.
168. Varga, S.M., and R.M. Welsh. 2000. High frequency of virus-specific interleukin-2-producing CD4<sup>+</sup> T cells and Th1 dominance during lymphocytic choriomeningitis virus infection. *J. Virol.* 74:4429-4432.
169. Lin, M.Y., L.K. Selin, and R.M. Welsh. 2000. Evolution of the CD8 T cell repertoire during infections. *Microbes and Infection* 2:1025-1039.
170. Welsh, R.M., J.M. McNally, M.A. Brehm, and L.K. Selin. 2000. Consequences of crossreactive and bystander CTL responses during viral infections. *Virology* 270:4-8.
171. McNally, J.M., C.C. Zarozinski, M.Y. Lin, and R.M. Welsh. 2001. Attrition of bystander T cells during virus-induced T cell and interferon responses. *J. Virol.* 75:5965-5976.
172. Szomolanyi-Tsuda, E., J.D. Brien, J.E. Dorgan, R.L. Garcea, R.T. Woodland, and R.M. Welsh. 2001. Antiviral T cell-independent type 2 antibody responses induced in vivo

in the absence of T and NK cells. *Virology*. 280:160-168.

173. Turgeon, N.A., N.N. Iwakoski, N.E. Phillips, W.C. Meyers, R.M. Welsh, D.L. Greiner, J.P. Mordes, and A.A. Rossini. 2000. Viral infection abrogates CD8<sup>+</sup> T cell deletion induced by costimulation blockade. *J. Surg. Res.* 93:63-69.
174. Kiessling, R., G. Pawelec, R.M. Welsh, J.D. Barry, and S. Ferrone. 2000. Have tumor cells learnt from microorganisms how to fool the immune system? *Molecular Medicine Today* 6:344-346.
175. Varga, S.M., L.K. Selin and R.M. Welsh. 2001. Independent regulation of T cell memory pools: relative stability of CD4 memory under conditions of CD8 memory T cell loss. *J. Immunol.* 166:1554-1561.
176. Szomolanyi-Tsuda, E., M.S. Brehm, and R.M. Welsh. 2002. Acquired immunity against virus infections. In: S.H.E. Kaufman, A. Sher and R. Ahmed, Eds. *The anti-infective immune response*. American Society of Microbiology Press, Washington, D.C., p. 247-265.
177. McNally, J.M. and R.M. Welsh. 2002. Bystander T cell activation and attrition. *Curr. Top. Microbiol. Immunol.* 263:29-41.
178. Welsh, R.M. 2001. Assessing CD8 T cell number and dysfunction in the presence of antigen. *J. Exp. Med.* 193:F19-22.
179. Daniels, K.A., G. Devora, W.C. Lai, C.L. O'Donnell, M. Bennett, and R.M. Welsh. 2001. Murine cytomegalovirus is regulated by a discrete subset of natural killer cells reactive with monoclonal antibody to Ly49H. *J. Exp. Med.* 194:29-44.
180. Varga, S.M., X. Wang, R.M. Welsh and T.J. Braciale. 2001. Immunopathology in RSV infection is mediated by a discrete oligoclonal subset of antigen-specific CD4<sup>+</sup> T cells. *Immunity* 15:637-646.
181. Welsh, R.M. 2001. Brief encounter. *Nature* 411:541-542.
182. Chen, H.D., A.E. Fraire, I. Joris, M.A. Brehm, R.M. Welsh, and L.K. Selin. 2001. Memory CD8<sup>+</sup> T cells in heterologous antiviral immunity and immunopathology in the lung. *Nat. Immunol.* 2:1067-1076.
183. Welsh, R.M., S.E. Stepp, E. Szomolanyi-Tsuda, C.D. Peacock, 2002. Tumor viral escape from inhibited T cells. *Nat Immunol.* 3:112-114.
184. Forman D., R.M. Welsh, T.G. Markees, B.A. Woda, J.P. Mordes, A.A. Rossini, 2002. Viral abrogation of stem cell transplantation tolerance causes graft rejection and host death by different mechanisms. *J Immunol.* 168:6047-6056.
185. Brehm, M.A., A.K. Pinto, K.A. Daniels, J.P. Schneck, R.M. Welsh, L.K. Selin,

2002. T cell immunodominance and maintenance of memory regulated by unexpectedly cross-reactive pathogens. *Nat. Immunol.* 3:627-634
186. Welsh, R.M. and L.K. Selin, 2002. No one is naive: The significance of heterologous T cell immunity. *Nat. Rev. Immunol.* 2:417-426.
187. Kim, S.-K., M.A. Brehm, R.M. Welsh, and L.K. Selin. 2002. Dynamics of memory T cell proliferation under conditions of heterologous immunity and bystander stimulation. *J. Immunol.* 169:90-98.
188. Brehm, M.A., T.G. Markees, K.A. Daniels, D.L. Greiner, A.A. Rossini, and R.M. Welsh. 2003. Direct visualization of cross-reactive effector and memory allo-specific CD8 T cells generated in response to viral infections. *J. Immunol.* 170:4077-4086.
189. Wang, X.Z., S.E. Stepp, M.A. Brehm., H.D. Chen, L.K. Selin, and R.M. Welsh. 2003. Virus-specific CD8 T cells in peripheral tissues are more resistant to apoptosis than those in lymphoid organs. *Immunity* 18:631--642.
190. Peacock, C.D., S.-K. Kim, and R. M. Welsh. Memory T cell attrition: reduced capacity of bona-fide memory CD44<sup>hi</sup> CD8<sup>+</sup> T cells to respond to homeostatic and poly I:C-induced proliferation. *J. Immunol.* 171:0000-0000 (in press) .
191. Zipris, D., R.M. Welsh, J.P. Mordes, J.X. Xie, D.L. Greiner, and A.A. Rossini. Infections that induce autoimmune diabetes in BBDR rats modulate CD4<sup>+</sup> CD25<sup>+</sup> T regulatory cell populations. *J. Immunol.* 170:3592-3602.
192. Peacock, C.D., W. Xu, S.E. Stepp, and R.M. Welsh. 2002. Dynamics of LY49 expressing cytotoxic lymphocyte subsets in response to infection. *Microbes and Infection* 4:1481-1490.
193. Welsh, Raymond M., Stepp, Susan E., Szomolanyi-Tsuda, Eva. 2003. B cell memory: Sapping the T cell. *Nature Medicine.* Vol.9, 2:164-166.